

TAXONOMIC INFRASTRUCTURE OF *SOLIDAGO* AND *OLIGONEURON*
(ASTERACEAE: ASTEREA) AND OBSERVATIONS ON THEIR
PHYLOGENETIC POSITION

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ABSTRACT

Among *Solidago* and its closest relatives (the subtribe Solidaginiinae, *sensu stricto*), *Solidago* itself is characterized primarily by its non-punctate, often coarsely toothed leaves and thyrsoid or secund capitulescence. Based on morphological features, the genus is formally divided into sections and subsections: sect. *Solidago* (four subsections) and sect. *Unilaterales* (seven subsections). Series are formally designated within some of the subsections. Typification is clarified for formally published names from older literature, and these are either incorporated in the active nomenclature or relegated to synonymy. The monotypic segregate genera *Brintonia* and *Brachychaeta* are treated as synonyms within sect. *Solidago* and sect. *Unilaterales*, respectively. Two genera previously treated within *Solidago* are here regarded as distinct, *Oreo-chrysum* Rydberg (monotypic) and *Oligoneuron* Small (six species). All three of these genera are hypothesized to be phylogenetically basal or near-basal members of the subtribe. In addition to new combinations proposed for the infrageneric taxonomy of *Solidago* and *Oligoneuron*, several others at lower ranks are necessary: *Oligoneuron album*, *O. houghtonii*, *O. rigidum* var. *glabratum*, *O. rigidum* var. *humilis*, as well as others for previously named interspecific hybrids within *Oligoneuron*. "×*Solidaster*" is hypothesized to be an intergeneric hybrid between *Oligoneuron album* and *Euthamia graminifolia*.

KEY WORDS: *Solidago*, *Oligoneuron*, *Oreo-chrysum*, ×*Solidaster*, Asteraceae, Astereae

Solidago L. is a genus of considerable morphological complexity with a long taxonomic history, but there has been no attempt since de Candolle

(1836) and Gray (1882) to present a taxonomic overview of the whole genus, and those bear little resemblance to the one presented here. A number of infrageneric categories at various ranks have been proposed, but all studies of the genus after Asa Gray's synoptical treatments in 1882 and 1884 have been regional or have dealt with only a portion of the taxa. Several segregates of *Solidago*, previously treated at various ranks within the genus, are now generally recognized as distinct genera: *Euthamia* (Nutt.) Nutt., *Chrysoma* Nutt., and *Petradoria* E. Greene (see Nesom 1991c and Nesom *et al.* 1990 for an overview of their phylogenetic placement; all three are within the subtribe Solidagininae). Two other segregates, which have been more generally and recently accepted within *Solidago*, are also excluded in the present treatment: *Oligoneuron* Small and *Oreochrysum* Rydberg. Reasons for their exclusion are given below. The classification of *Solidago* presented here surely will be subject to modification, but it offers a more comprehensive and clearly defined point of reference than has been available for more than a century.

Solidago includes a total of about 80-90 species in North America (including México), with an additional 10-20 of sect. *Solidago* native to Eurasia. Because of taxonomic difficulties among the Old World taxa, they have not been included in the present treatment, but aspects of their taxonomy and variation are discussed below. One other species (*S. microglossa* DC. of sect. *Unilaterales*) is autochthonous in South America (Nesom in prep.) and naturalized in Africa. A number of North American species are naturalized and cultivated in Asia and in Europe, where they are highly regarded as ornamentals. The greatest number of species and the greatest morphological diversity in the genus occur in eastern North America, and its closest generic relatives occur there as well (as hypothesized by Nesom 1991c, the present study, and in prep.).

The base chromosome number of *Solidago* is $x=9$, without exception, as evidenced by hundreds of reports (summary by Semple 1992). Polyploidy is common within and among species. The karyotype appears to be relatively uniform across all groups (*e.g.*, Kapoor & Beaudry 1966; Beaudry 1970b; Kapoor 1975), with a predominance of chromosomes with submedian centromeres.

In the following taxonomic outline, the lists of constituent species sometimes differ from recently proposed taxonomy. Some of the names used may be justifiably applied at a lower rank, but they are included here as species for ease of reference. I have tried to include names in relatively recent use, but the species lists are not an attempt to present a summary of accepted nomenclature; there appears to be little consensus regarding the taxonomy of many subgroups in the genus. Recent references, where available, are provided as guides to definitions of species boundaries, but a large amount of fragmentary literature exists, and there are but few modern, documented, taxonomic summaries of any groups of *Solidago*. Contemporary regional floras provide the best and often only means of identification (those with literature citations

are particularly helpful, e.g., Semple & Ringius 1983, rev. Semple 1992; Taylor & Taylor 1984).

In the application of names published by Torrey & Gray (1842) and by Gray (1884), I have followed the precedent of Holmgren (1979) and Jones (1980). The nomenclature in Gray's synopsis of *Solidago* (1882) is nearly identical to his treatment in the *Synoptical Flora* (1884), and I have considered the earlier work as the first publication for some of the names. Some names of sections and series are adopted from Loudon's *Hortus Britannicus*, following the notice of Sundberg & Jones (1987, 1988). Published names of numerous "species-groups," for which a clearly indicated rank was not provided, can be found in various publications, particularly in Rydberg (1917, 1932) and Mackenzie (1933). I have used some of these as basionyms. All of Rafinesque's generic segregates from *Solidago* are accounted for, except *Aplactis* Rafin. (*Fl. Tellur.* 2:42. 1836 [1837]), which was lectotypified as a synonym of *Chrysoma* by Kapoor & Beaudry (1966). There do not appear to be any taxonomic categories for the Eurasian taxa that would impinge on the nomenclature presented here.

The two main infrageneric groups of *Solidago* are treated as sections, as the use of "subgenus" generally implies a more profound difference than is found within *Solidago* as treated here. Hybridization is relatively common in various parental combinations among species of the subsections as well as between the two sections. The nature of interrelationships among the species groups is not clear, and several of the subsections of sect. *Solidago* might justifiably be treated at a higher rank. Below the rank of section, I have used subsection as the primary taxonomic category, because smaller species groups (series) are recognized within some of the subsections, and other groups evidently exist also, even where they have not been accorded a formal name in this treatment.

Solidago L., *Sp. Pl.* (ed. 1) 878. 1753. LECTOTYPE: *Solidago virgaurea* L. (Britton & Brown, *Illust. Fl. N. U.S.*, ed. 2, 3:380. 1913.)

1. *Solidago* sect. *Solidago*

Solidago subg. *Virgaurea* (DC.) Torr. & Gray, *Fl. N. Amer.* 2:197. 1842. Not Tamamsch. 1959. *Solidago* sect. *Virgaurea* DC., *Prodr.* 5:330. 1836. Torrey & Gray attributed the subgeneric combination to de Candolle, but de Candolle clearly referred to the group as "sect. *Virgaurea*." TYPE: *Solidago virgaurea* L.

Capitulescence branches very short and axillary to longer and ascending, the heads more or less uniformly distributed around the head-bearing branch-

lets, not at all secund, the capitulescence axillary and discontinuous or more nearly terminal and elongate-spicate to somewhat corymboid.

a. *Solidago* subsect. *Solidago*

Solidago sect. *Virgaurea* DC., *Prodr.* 5:330. 1836. TYPE:
Solidago virgaurea L.

Amphirhapis DC., *Prodr.* 5:343. 1836. [pro parte; Hooker & Jackson 1895]. TYPE: not designated

Actipsis Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. LECTOTYPE, designated here: *Solidago glomerata* Michx.

Solidago sect. *Erectae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. *Solidago* [sect. *Virgaurea*] series *Erectae* (G. Don) DC., *Prodr.* 5:335. 1836. TYPE: *Solidago erecta* Pursh.

Solidago [sect. *Erectae*] ser. *Serratae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago virgaurea* L.

Solidago [sect. *Thyrsiflorae*] ser. *Pauciradiatae* Juz., *Fl. URSS* 25:34. 1959. LECTOTYPE, designated here: *Solidago virgaurea* L.

Solidago [sect. *Thyrsiflorae*] ser. *Multiradiatae* Juz., *Fl. URSS* 25:47. 1959. TYPE: *Solidago multiradiata* Ait.

Species included (10): *Solidago calcicola* (Fernald) Fernald, *S. cutleri* Fernald, *S. glomerata* Michx., *S. multiradiata* Ait., *S. nana* A. Gray, *S. plumosa* Small, *S. sciaphila* Steele, *S. simplex* Kunth (incl. *S. bellidifolia* E. Greene, *S. chlorolepis* Fernald, *S. deamii* Fernald, *S. decumbens* E. Greene, *S. gillmanii* [A. Gray] Steele, *S. glutinosa* Nutt., *S. neomexicana* Woot. & Standl., *S. oreophila* Rydb., *S. racemosa* E. Greene, *S. randii* [Porter] Britt., and *S. victorinii* Fernald), *S. spathulata* DC., *S. spithamaea* M.A. Curtis, and some of the autochthonous Old World taxa, including *S. virgaurea* L. – see comments below (Cronquist 1947; Wagenitz 1979; Ringius 1985, 1987; Ringius & Semple 1987, 1991; Nesom 1989b).

Rhizomes short, thick; leaves thick to thin, sometimes glutinous, glabrous to sparsely hairy, shallowly crenate to sharply serrate, net-veined, oblanceolate to obovate, attenuate to a short petiolar region, the basal usually persistent, cauline reduced upward; heads in a cylindrical to ellipsoidal thyrse, distinctly corymboid in *Solidago cutleri*, *S. multiradiata*, and *S. spithamaea*; phyllaries 1-veined; achenes mostly pubescent; pappus bristle apices attenuate.

Solidago glomerata has been hypothesized to be closely related to *S. squarrosa* (Beaudry 1963), but the thick, oblanceolate leaves and thick phyllaries with rounded apices of the former indicate, instead, that it belongs with subsect. *Solidago*. Like *S. spithamaea*, *S. glomerata* appears to be an isolated

relict harbored within the high Appalachians. Several species groups might be recognized within subsect. *Solidago*.

All of the native Old World taxa of *Solidago* are in sect. *Solidago*, but there is a great deal of morphological variability that appears to be poorly understood taxonomically. The greatest range of variation is in eastern Asia, where the capitulescences range from axillary to a broad or narrow thyrse to a relatively compact, terminal cluster. The leaves vary in thickness and in shape from ovate with a winged petiolate to elliptic-lanceolate and epetiolate. Only rarely do the leaves have a strong basal disposition. Many of these forms have been classified within *S. virgaurea*, whereas in North America they would be identified as different species and even placed in different subsections. See further comments below in the "Review of the *S. virgaurea* complex."

b. *Solidago* subsect. *Albigula* (Rafin.) Nesom, *comb. et stat. nov.*

BASIONYM: *Solidago* subg. *Albigula* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. TYPE: *Solidago bicolor* L.

Solidago subg. *Chrysastrum* Torr. & Gray, *Fl. N. Amer.* 2:195. 1842. *Solidago* sect. *Chrysastrum* (Torr. & Gray) A. Gray, *Proc. Amer. Acad. Arts* 16:80. 1880. LECTOTYPE, designated here: *Solidago squarrosa* Muhl.

Solidago sect. *Squarrosae* A. Gray, *Proc. Amer. Acad. Arts* 17:189. 1882. TYPE: *Solidago squarrosa* Muhl.

Solidago ser. *Integrifoliae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE: *Solidago erecta* Pursh.

Anactis Rafin., *Fl. Tellur.* 2:44. 1836. [1837]. Not Cass. 1827. TYPE: *Solidago discoidea* (Ell.) Torr. & Gray.

Brintonia E. Greene, *Erythea* 3:89. 1895. TYPE: *Solidago discoidea* (Ell.) Torr. & Gray.

Species included (9): *Solidago bicolor* L., *S. discoidea* (Ell.) Torr. & Gray, *S. erecta* Pursh, *S. hispida* Muhl., *S. macrophylla* Pursh, *S. porteri* Small, *S. puberula* Nutt., *S. roanensis* Porter, *S. squarrosa* Muhl. (Greene 1895; Monachino 1955; Semple & Ringius 1983).

Rhizomes short; leaves hairy, crenate to serrate or entire, net-veined, oblanceolate to narrowly ovate, attenuate to a relatively long petiole, not clasping, the basal persistent, cauline reduced upward; heads mostly in a terminal, elongated and narrow capitulescence, more or less leafy bracteate toward the base, the lower clusters often becoming elongate and stiffly ascending; phyllaries 1-veined; achenes glabrous or less commonly very sparsely strigose; pappus bristle apices strongly clavate in *Solidago bicolor* and *S. discoidea*, seen only as a slight tendency in the other species.

Solidago bicolor and *S. discoidea*, both of which produce white corollas and strongly clavate pappus bristle apices, have been postulated to be allopatric,

sister species (Nesom 1991c), even though *S. bicolor* hybridizes and perhaps intergrades with *S. hispida* (e.g., Ringius & Semple 1983). The strongly squarrose phyllaries of *S. squarrosa* are distinctive but a similar tendency also exists in *S. erecta* and *S. discoidea*, as well as *S. macrophylla*. These species are among the relatively few in *Solidago* to produce thin phyllaries with narrowly acute apices; the phyllary apices in *S. erecta* tend to be rounded.

The position of *Solidago macrophylla* is problematic. It is tentatively included here in subsect. *Albigula* on the basis of its short rhizomes, leaf morphology and disposition, phyllaries with acute, sometimes squarrose apices, and glabrous achenes. It stands apart from these species, however, and most others in the genus, in its combination of long style appendages, very large heads, carinate phyllaries, and short disc corolla lobes. Dr. L. Brouillet has pointed out to me that *S. macrophylla* is more similar to the plants of subsect. *Glomeruliflorae* in its relatively mesic habitat, and its capitulescence varies from the terminal-virgate characteristic of subsect. *Albigula* to strictly axillary, as in subsect. *Glomeruliflorae*. In yet another possibility, Fernald (1908) observed that *S. macrophylla* was the "nearest American ally" of the Eurasian *S. virgaurea* (subsect. *Solidago*), although he later (1950) changed his mind about this. See further comments below in the "Review of the *S. virgaurea* complex."

- c. *Solidago* subsect. *Glomeruliflorae* (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sect. *Glomeruliflorae* Torr. & Gray, *Fl. N. Amer.* 2:197. 1842. LECTOTYPE, designated here: *Solidago caesia* L.

Leioligo subg. *Breviligula* Rafin., *Fl. Tellur.* 2:42. 1836. [1837].
LECTOTYPE, designated here: *Solidago caesia* L.

Solidago subg. *Pleiaetila* Rafin., *Fl. Tellur.* 2:42. 1836. [1837].
LECTOTYPE, designated here: *Solidago flexicaulis* L.

Species included (7): *Solidago albopilosa* L. Braun, *S. caesia* L., *S. curtisii* Torr. & Gray, *S. flaccidifolia* Small, *S. flexicaulis* L., *S. lancifolia* (Torr. & Gray) Cham., *S. ouachitensis* C. & J. Taylor (Andreasen & Eshbaugh 1973; Chmielewski & Semple 1985; Chmielewski *et al.* 1989; Semple *et al.* 1984; Taylor & Taylor 1983, 1986)

Rhizomes usually elongated, creeping; leaves lanceolate to oblanceolate, commonly abruptly narrowed to a winged petiole, net-veined, serrate, the basal not persistent, cauline only gradually reduced upward; lower heads in distantly separated axillary clusters shorter than the subtending leaves, the upper sometimes spicately arranged; phyllaries 1-veined (sometimes 3-5-nerved in *Solidago curtisii*); achenes densely pubescent; pappus bristle apices attenuate. Different from subsect. *Albigula* in its elongate rhizomes, absence of basal leaves, short axillary floral clusters, and hairy achenes.

- d. *Solidago* subsect. *Thyrsiflorae* (A. Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sect. *Thyrsiflorae* A. Gray, Proc. Amer. Acad. Arts 17:190. 1882. Not Tamamsch. 1959. *Solidago* ser. *Thyrsiflorae* (A. Gray) Hoffm., Pflanzenf. 4(5):150. 1889. LECTOTYPE, designated here: *Solidago wrightii* A. Gray.

Leioligo Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago petiolaris* Ait.

Leioligo subg. *Doria* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago petiolaris* Ait.

Leioligo subg. *Liniuque* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago speciosa* Nutt.

Species included (6): *Solidago buckleyi* Torr. & Gray, *S. hintoniorum* Nesom, *S. orientalis* (Nesom) Nesom, *S. petiolaris* Ait., *S. speciosa* Nutt. (incl. *S. harperi* Mackenzie, *S. jejunifolia* Steele), *S. wrightii* A. Gray (Nesom 1990; Taylor & Taylor 1986).

Rhizomes mostly short, sometimes lengthening; basal leaves not persistent, the cauline gradually reduced upward, broadly to narrowly elliptic to oblanceolate, sessile or with a very short petiole, serrulate to nearly entire, distinctly thickened to coriaceous, net-veined, glabrous to hairy, sometimes glandular (sessile or stipitate); capitulescence elongated, sometimes broad, sometimes somewhat punctuated in the lower portion (in *Solidago buckleyi*), loosely but distinctly corymboid in *S. wrightii*; phyllaries 1(-3)-veined, commonly stipitate-glandular or glutinous; achenes glabrous or with a few hairs; pappus bristles commonly slightly but distinctly dilated toward the apex.

Anderson & Creech (1975) noted a similarity in leaf morphology between *Oligoneuron* and taxa of subsect. *Thyrsiflorae*. This may be reflective of the relatively primitive position of the latter within *Solidago*. Plants of subsect. *Thyrsiflorae* also are the only ones in the genus to produce prominent stipitate glands, another feature suggestive of a primitive position for these species, if the stipitate glands are homologous with the sunken ones (punctae) characteristic of the rest of the subtribe. This is clearly the case in at least some other *Astereae* (e.g., *Isocoma* Nutt., see comments in Nesom 1991d).

2. *Solidago* sect. *Unilaterales* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. *Solidago* ser. *Unilaterales* (G. Don) DC., *Prodr.* 5:330. 1836. LECTOTYPE, designated here: *Solidago canadensis* L.

Dr. Semple (pers. comm.) has noted that the identification of specimens listed by Loudon may be problematic, with corresponding problems in typification. The name chosen by Don, however, for

this section (sect. *Unilaterales*) appears to be so appropriate for the secund capitulescence that there could be little doubt what group of species he was referring to. Even if some other species were chosen as the lectotype, the application of the name would not change.

Solidago sect. *Paniculatae* A. Gray, Proc. Amer. Acad. Arts 17:191. 1882. Not Tamamsch. 1959. LECTOTYPE, designated here: *Solidago canadensis* L.

Capitulescence branches ascending-recurved with the heads usually in a distinctly secund arrangement, the capitulescence dense and pyramidal or more open with the branches relatively widely separated.

a. *Solidago* subsect. *Triplinerviae* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts 17:195. 1882. *Solidago* sect. *Triplinerviae* Torr. & Gray, *Fl. N. Amer.* 2:222. 1842. LECTOTYPE, designated here: *Solidago canadensis* L.

Solidago ser. *Trinerves* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago canadensis* L.

Solidago subg. *Brachyactis* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago canadensis* L.

Species included (13): *Solidago altiplanites* C. & J. Taylor, *S. altissima* L., *S. canadensis* L., *S. durangensis* Nesom, *S. gigantea* Ait., *S. gypsophila* Nesom, *S. juliae* Nesom, *S. leavenworthii* Torr. & Gray, *S. lepida* DC. (perhaps incl. *S. elongata* Nutt.), *S. microglossa* DC., *S. paniculata* DC., *S. rupestris* Rafin., *S. shortii* Torr. & Gray (Beaudry 1963, 1964, 1970a; Croat 1967, 1972; Melville & Morton 1982; Morton 1984; Taylor & Taylor 1983; Nesom 1989a, 1989d, 1991a; Semple *et al.* 1984, 1990).

Rhizomes elongate, creeping (short in *Solidago shortii*); leaves serrulate, 3-nerved, lanceolate, even-sized and densely arranged along the stem, the basal not persistent; heads densely arranged in a pyramidal panicle; phyllaries 1-veined; achenes pubescent; pappus bristle apices attenuate.

b. *Solidago* subsect. *Nemorales* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Nemorales* Mackenzie in Small, *Man. Southeast. Fl.* 1348. 1933. TYPE: *Solidago nemoralis* Ait.

Species included (5): *Solidago macvaughii* Nesom, *S. mollis* Bartl., *S. nana* Nutt., *S. nemoralis* Ait. (incl. *S. decemflora* DC.), *S. velutina* DC. (incl. *S.*

arizonica [A. Gray] Woot. & Standl., *S. californica* Nutt., *S. sparsiflora* DC.) (Nesom 1989c; Semple *et al.* 1990, 1992).

Rhizomes short; basal leaves persistent, the cauline strongly reduced upward, oblanceolate, gradually attenuate to a petiolar region, 3-veined (sometimes obscurely so in *Solidago nemoralis*), serrulate, not clasping, usually densely hairy; capitulescence sometimes pyramidal, commonly more loosely arranged; phyllaries 1-veined; achenes hairy; pappus bristle apices attenuate.

- c. *Solidago* subsect. *Venosae* (G. Don) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* ser. *Venosae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago rugosa* Miller.

Species included (8): *Solidago aestivalis* Bicknell, *S. aspera* Ait. (incl. *S. celtidifolia* Small, *S. drummondii* Torr. & Gray), *S. fistulosa* Mill., *S. latisimifolia* Miller (= *S. eliottii* Torr. & Gray; incl. *S. edisoniana* Mackenzie, *S. mirabilis* Small), *S. microphylla* (A. Gray) Engelm. *ex* Small (incl. *S. delicatula* Small), *S. radula* Nutt., *S. rugosa* Miller, *S. ulmifolia* Muhl. (Fernald 1936; Beaudry 1960, 1963, 1969; Semple *et al.* 1984; Uttal & Porter 1988).

Rhizomes elongate, creeping (except in *Solidago ulmifolia* and *S. microphylla*); basal leaves not persistent, the cauline relatively little reduced upward until the capitulescence, net-veined, serrulate, sparsely hairy, broadly elliptic, sessile or short-petiolate, sometimes subclasping; capitulescence loose, sometimes loosely pyramidal; phyllaries 1-veined; achenes hairy; pappus bristle apices attenuate.

Different from subsect. *Nemorales* in its creeping rhizomes, net-veined leaves, the basal not persistent, the cauline not reduced upward. *Solidago radula* is placed here because of its creeping rhizomes and primarily cauline leaves, but its leaves sometimes are 3-nerved and the species may be more closely allied to those of subsect. *Nemorales*. Overall, however, subsect. *Venosae* is probably more closely related to subsect. *Argutae*, the primary difference being leaf disposition; the two subsections might justifiably be combined into a single one with three series.

- d. *Solidago* subsect. *Argutae* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Argutae* Mackenzie in Small, *Man. Southeast. Fl.* 1347. 1933. TYPE: *Solidago arguta* Ait.

Solidago sect. *Secundiflorae* Torr. & Gray, *Fl. N. Amer.* 2:212. 1842. LECTOTYPE, designated here: *Solidago arguta* Ait.

Rhizomes short (slender stolons in *Solidago ludoviciana* and *S. sphacelata*); leaves commonly doubly and coarsely serrate, net-veined, hairy to glabrous,

the basal and lower usually persistent, with a long, winged petiole, the cauline reduced upward and mostly epetiolate; heads in a loose and open capitulescence; phyllaries 1-veined; achenes sparsely hairy to glabrous; pappus bristle apices attenuate.

- * *Solidago* ser. *Argutae* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Argutae* Mackenzie in Small, *Man. Southeast. Fl.* 1347. 1933. TYPE: *Solidago arguta* Ait.

Species included (5): *Solidago arguta* Ait. (incl. *S. harrisii* Steele, *S. yadkinensis* [Porter] Small, *S. boottii* Hook.), *S. ludoviciana* (A. Gray) Small (incl. *S. salicina* Ell., *S. strigosa* Small), *S. patula* Muhl., *S. tarda* Mackenzie, *S. verna* Curtis ex Torr. & Gray (Morton 1974).

Basal and lower leaves usually broadly lanceolate, basally attenuate to a winged petiole, the cauline reduced upward; ray flowers relatively numerous; pappus bristles not markedly shortened.

- * *Solidago* ser. *Brachychaetae* (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Brachychaeta* Torr. & Gray, *Fl. N. Amer.* 2:194. 1842. TYPE: *Solidago sphacelata* Rafin.

Species included (3): *Solidago auriculata* Shuttlew. ex Blake, *S. brachyphylla* Chapman, *S. sphacelata* Rafin.

Basal and lower leaves usually ovate, basally cordate to truncate, with a winged petiole, the cauline strongly reduced upward; ray flowers absent or very few (1-3); pappus bristles markedly shortened.

- e. *Solidago* subsect. *Odorae* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Odorae* Mackenzie in Small, *Man. Southeast. Fl.* 1346. 1933. TYPE: *Solidago odora* Ait.

Species included (2): *Solidago chapmanii* Torr. & Gray, *S. odora* Ait. (Cronquist 1977).

Rhizomes short, hairs in lines along the stem, basal leaves not persistent, the cauline numerous, linear to narrowly lanceolate, basally attenuate, sessile, entire, net-veined, glabrous, punctate-glandular; capitulescence loose; phyllaries 1-veined; achenes slightly hairy to glabrate; pappus bristle apices attenuate.

The punctate-glandular leaves of these two species are unique in the genus; no other *Solidago* are punctate-glandular. They are different in anatomy from punctate glands consistently produced in most other species of *Solidagininae* (Anderson & Creech 1975) but perhaps represent the same, ancestral, genetic

potential. *Solidago odora* and *S. chapmanii*, which are sometimes treated as a single species, are similar in habit and perhaps most closely related to the plants of subsect. *Junceae*.

f. ***Solidago* subsect. *Junceae*** (Rydb.) Nesom, *comb. et stat. nov.*

BASIONYM: *Solidago* sp.-group *Junceae* Rydb., *Fl. Prairie & Plains* 792. 1932. TYPE: *Solidago juncea* Ait.

Rhizomes long and stoloniform (shorter in *Solidago pinetorum* and *S. gattingeri* and in ser. *Spectabiles*); basal and lower cauline leaves commonly persistent, linear to narrowly and sharply lanceolate, often somewhat falcate, sessile to obscurely petiolate, 3-nerved (obscurely or sometimes 1-veined in *S. tortifolia* and *S. gattingeri*), entire to remotely serrate, glabrous or slightly hairy, the cauline usually reduced upward (more strongly developed in *S. tortifolia*); capitulescence relatively dense in *S. juncea*, *S. missouriensis*, and *S. tortifolia*, looser in *S. pinetorum* and *S. gattingeri*, flat-topped in *S. ericamerioides*, relatively dense and usually not perceptibly secund in ser. *Spectabiles*; phyllaries 1-veined; achenes glabrous to sparsely hairy; pappus bristle apices attenuate.

* ***Solidago* ser. *Junceae*** (Rydb.) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Junceae* Rydb., *Fl. Prairie & Plains* 792. 1932. TYPE: *Solidago juncea* Ait.

Solidago subg. *Triactis* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago tortifolia* Ell.

Species included (7): *Solidago ericamerioides* Nesom, *S. gattingeri* Chapman, *S. juncea* Ait., *S. missouriensis* Nutt., *S. pinetorum* Small, *S. pringlei* Fernald (incl. *S. muelleri* Standley), *S. tortifolia* Ell. (Nesom 1989a; Semple *et al.* 1992).

Chaffy bracts are produced on the receptacles of *Solidago juncea* (Morton 1968) and *S. missouriensis* (Cronquist 1980) as well as *S. confinis*. These structures are similar to the inner phyllaries, and their occurrence clearly is derived within the genus. *Solidago juncea* and *S. missouriensis* are similar in other features and probably are sister species. *Solidago missouriensis* consistently produces slender stolons, while *S. juncea* does not, but there is a distinct tendency in the latter for the rhizomes to lengthen (Cronquist 1980), and there is some evidence that the two species intergrade. Most of these species (particularly *S. missouriensis* and *S. pinetorum*) have a tendency to produce axillary fascicles of much reduced leaves; *S. pringlei* and *S. ericamerioides* do not. Natural hybrids between *S. juncea* and *S. nemoralis* have been noted by Beaudry (1969).

* *Solidago* ser. *Spectabiles* Nesom, ser. nov. TYPE: *Solidago spectabilis* A. Gray.

Differt a speciebus subsect. *Junceorum* (Rydb.) Nesom foliis parvulis caulinis in fasciculis axillaribus carentibus et capitulescentia relative densa plerumque non perceptibile secunda.

Species included (3): *Solidago confinis* A. Gray, *S. guiradonis* A. Gray, *S. spectabilis* (D.C. Eat.) A. Gray

Semple *et al.* (1992) observed that these three species form the "far western element of the *Solidago missouriensis/juncea* group of goldenrods," with which I agree. Ser. *Spectabiles* is a group well-defined geographically as well as morphologically, the plants particularly tall and with capitulescences that show only a weak tendency, if any, to be secund. Some of the species of ser. *Junceae* also show the same tendency in the capitulescence. The capitulescence of *S. ericamerioides* is flat-topped, but this Mexican gypsophile is highly reduced in stature and probably derived from *S. pringlei* (the latter identified as *S. missouriensis* in an earlier study (Nesom 1989a), which produces only a weakly secund capitulescence. The plants of ser. *Spectabiles* also resemble those of subsect. *Maritimae* (which see for further comments).

g. *Solidago* subsect. *Maritimae* (Torr. & Gray) A. Gray, *Synopt. Fl. N. Amer.* 2(1):149. 1884. *Solidago* sect. *Maritimae* Torr. & Gray, *Fl. N. Amer.* 2:211. 1842. LECTOTYPE, designated here: *Solidago sempervirens* L.

Solidago sect. *Virgatae* Torr. & Gray, *Fl. N. Amer.* 2:201. 1842. TYPE: *Solidago virgata* Michx. (= *S. stricta* Ait.).

Solidago subsect. *Unicostatae* A. Gray, *Synopt. Fl. N. Amer.* 2(1):149. 1884. LECTOTYPE, designated here: *Solidago gracillima* Torr. & Gray.

Lepiactis Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. TYPE: *Solidago virgata* Michx. (= *S. stricta* Ait.).

Solidago subg. *Stenactila* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago sempervirens* L.

Dasiorima Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. LECTOTYPE, designated here: *Solidago mexicana* L. (= *S. sempervirens* L.).

Species included (5): *Solidago gracillima* Torr. & Gray (incl. *S. austrina* Small, *S. flavovirens* Chapm., *S. perlonga* Fernald, *S. simulans* Fern.), *S. pulchra* Small, *S. sempervirens* L., *S. stricta* Ait., *S. uliginosa* Nutt. (incl. *S. chrysolepis* Fern., *S. neglecta* Torr. & Gray, *S. purshii* Porter, *S. uniligulata*

[DC.] Porter, *S. klughii* Steele) (Goodwin 1937; Beaudry 1963; Chmielewski *et al.* 1985).

Rhizomes short (slender stolons in *Solidago stricta*); leaves thick, mostly glabrous, net-veined, crenate-dentate, the basal and lower oblanceolate, persistent, cauline reduced but slightly upward (strongly reduced in *S. stricta*) and subclasping; heads mostly in a cylindric to narrowly rhomboid panicle but the lower branches commonly secund; phyllaries 1-veined; achenes pubescent to glabrous; pappus bristle apices attenuate.

These are the "marsh and bog goldenrods." There is a distinctive but apparently superficial habitual resemblance between subsect. *Maritimae* and subsect. *Junceae* ser. *Spectabiles*. Plants of both groups are mostly glabrous, entire-leaved, and produce an elongate capitulescence often with little evidence of a secund arrangement of heads. Those of ser. *Spectabiles*, however, differ in their upland habitat, axillary fascicles of small leaves, and lanceolate, non-clasping leaves without parallel lateral veins. Hybrids have been observed between *Solidago stricta* and *S. sempervirens* (Cronquist 1980).

REVIEW OF THE *SOLIDAGO VIRGAUREA* COMPLEX IN NORTH AMERICA AND EURASIA

In De Candolle's (1836) comprehensive treatment of *Solidago*, the brief descriptions of the Old World *S. virgaurea* L. (the generitype) and the New World *S. simplex* Kunth, *S. spathulata* DC., and *S. multiradiata* Ait. were by no means mutually exclusive. Torrey & Gray (1842) treated *S. virgaurea* (including *S. multiradiata* Ait.) as a member of the North American flora, and noted its occurrence from Arctic America and Labrador to the Rocky Mountains and to the White Mountains (New York and New Hampshire). They regarded it as (p. 207) "A very variable species, which in this country is confined to the Northern regions, and the higher mountains of the Northern States. Nearly all the American specimens belong either to the var. β [var. *ericetum*, sensu de Candolle], which very nearly approaches the var. *Cambrica* of Europe, or to the var. γ [var. *alpestris*, sensu de Candolle], which passes insensibly into other forms of this species, to which it should doubtless be united." Later, Gray (1867) restricted this concept somewhat but still recognized two North American varieties of *S. virgaurea*; yet later (1882, 1884), he had narrowed his view of the species in North America to a variable var. *alpina* Bigelow of the northeastern United States and adjacent Canada (this taxon strictly interpreted by Fernald [1908] as *S. cutleri* Fernald, which is very similar and perhaps not different from *S. multiradiata* var. *arctica* [DC.] Fernald). Gray explicitly noted, however, the occurrence of intergrades and problematic distinctions between *S. virgaurea* and related American taxa.

Porter (1893) described additional varieties of *Solidago virgaurea* from the northeastern United States, but he identified high elevation plants from the

White Mountains as the otherwise Old World *S. alpestris* Wald. & Kit. ex Willd. (= *S. virgaurea* var. *alpestris* [Wald. & Kit. ex Willd.] DC. The latter plants were equated by Ringius (1986) with *S. glutinosa* var. *monticola* (Porter) Ringius. Porter noted that (p. 210) "on comparing them with *S. alpestris* from the Swiss and Carpathian Alps of Europe and the Altai Mountains of Asia the differences are so slight that the two must be regarded as identical. And such a conclusion ought to cause no surprise, when we consider the notable company of Old World alpinists which occupy the same mountain-tops. This only adds one more to the number."

Fernald (1899) effected the last nomenclatural connection of North American plants to the Old World species, as he added another variety to *Solidago virgaurea* (var. *calcicola* Fernald). He later decided that this taxon could stand as a separate species (1908) and made the following observation (p. 87): "Recent detailed studies of types and authentic specimens of this group have convinced the writer that we have in eastern North America no plant which can satisfactorily be placed with the Eurasian *S. Virgaurea*. The nearest American ally of that species, as understood by the writer, is *S. macrophylla* Pursh . . ." He added the caveat, however (p. 87), that "*S. calcicola* also simulates forms of *S. Virgaurea*." Over the next 30 years (1915, 1927, 1936), Fernald described a number of new, narrowly endemic species that could be considered similar to *S. virgaurea*, and by 1950 (p. 1392), he had decided, in contrast to his earlier view, that *S. calcicola* rather than *S. macrophylla* is "Our closest approach to Eurasian *S. virgaurea* L.," although he did not specify what segment of this highly polymorphic species he was referring to. These apparently were Fernald's only published comments specifically referring to *S. virgaurea*.

In the early 1900's, with a proliferation of names for North American population systems, regional floristicians (e.g., Rydberg 1917; Wootton & Standley 1915; Friesner 1933) appear to have exclusively adopted the regional nomenclature for these goldenrods. By around mid-century, American floristic studies were, of necessity, strongly concerned with making sense of the accumulated regional names. The complete nomenclatural separation of the American populations from the Eurasian ones appears to have been made implicitly, tacitly (except for a few sentences by Fernald, see above), and primarily on a continental basis, as the American taxa became better known morphologically and geographically, and as they acquired their own complex set of regional nomenclature.

Cronquist (1947) provided a detailed review of a group of American taxa that included many associated historically with *Solidago virgaurea*. He noted the strong tendencies for intergradation among them and gathered them into a single species (*S. glutinosa* Nutt., with five varieties divided among two subspecies), which comprises a group of closely related taxa spread over much of the northern half of North America, and extending southward along the Rocky Mountain cordillera into Colorado and New México, and from there further

south into central México along the Sierra Madre Oriental. Cronquist soon completely revised this nomenclature (Cronquist in Gleason 1952; Cronquist 1955), as he broadened the *S. glutinosa* complex by including the earlier-named *S. spathulata* DC. of the Pacific coast.

Ringius (1986) and Ringius & Semple (1987) recently completed cytological studies and multivariate morphological analyses of the taxa of the *Solidago glutinosa* complex (separate from *S. spathulata*, in their view; also in the view of Keck [1960]). Ringius recognized seven varieties in two subspecies, for the most part adopting Cronquist's basic concepts and taxonomy (of 1947) regarding the complex, but the realization that *S. simplex* is an older name for the same species (Nesom 1989) prompted yet another nomenclatural reorganization of the whole group (Ringius & Semple 1991). The numerical analyses confirmed Cronquist's observation that the taxa of the complex, though identifiable, were separated by differences "only in averages." The added cytological data were significant in showing that members of subsp. *simplex* are diploid ($n=9$), while members of subsp. *randii* (Porter) Ringius are chiefly tetraploid ($n=18$). Old World *S. virgaurea* is known only at the diploid level (Huziwara 1962; Wagenitz 1976).

Solidago multiradiata Ait. is similar to *S. simplex* and the two species apparently hybridize in high elevation habitats of the Rocky Mountains (Ringius 1986). The former has an American distribution nearly as broad as the *S. simplex* complex, occurring from Alaska southward into California, Arizona, and New Mexico, and southeastward into Labrador, Newfoundland, Nova Scotia, and the Gaspé Peninsula of Québec; it lacks a southward extension into México known for *S. simplex*. Tamamschyan (1959) included *S. multiradiata* var. *arctica* (DC.) Fernald as a member of the Siberian flora (as *S. compacta* Turcz.), and Hultén (1968) showed its distribution extending westward from Alaska across the Bering Strait.

Despite the numerous nomenclatural juxtapositions and their implications regarding possible evolutionary relationships between the American and Old World plants of the *Solidago virgaurea* complex, neither Cronquist nor Ringius & Semple have considered (in literature) the nature of their relationship. In recent accounts of the European flora (Wagenitz 1979; Clapham *et al.* 1987) and the Japanese flora (Kitamura 1965), the *S. virgaurea* complex is said to occur in North America. Indeed, close analogs for many eastern American plants of the *S. glutinosa* complex, as well as other taxa, can be found among Eurasian ones. The autochthonous origin and continental endemism of the North American taxa can be accepted as a pragmatic hypothesis until the complex can be studied from a broader perspective, but it seems likely that the relationship between Old and New World taxa may prove closer than currently recognized in American treatments.

I agree with Fernald (see above) that *Solidago macrophylla* and *S. calicicola* both approach the morphology of typical *S. virgaurea*, judging from three

specimens in the Linnaean herbarium (LINN) identified as the latter (LINN-fiche: 998.15-17). I also agree with his eventual elimination of *S. macrophylla* from such consideration, as there are not any Old World taxa with its distinctive floral and capitular features. A fourth Linnaean specimen identified as *S. virgaurea* (998.18) has more or less entire leaves in a basal cluster and is more similar to plants of the *S. simplex* complex. The wide variation (habit, leaf disposition, capitulescence form) in what is currently accepted as *S. virgaurea* suggests that the distinctions I have made among New World subsections of sect. *Solidago* may be artificial. Even the assignment of *S. virgaurea* itself to one of the New World groups is problematic.

The geographic range of *Solidago virgaurea* (sensu lato, as recently considered) extends from the west coast of Europe immediately north into Arctic regions, south as far as North Africa, to the east coast of Asia as far north as the Bering Sea islands. Subsp. *virgaurea* occurs widely throughout Europe, to North Africa and western Asia in the Caucasus and western Siberia (Wagenitz 1979). The geographic distinction of subsp. *virgaurea* from subsp. *minuta* (L.) Arcangeli is not clear, but the latter is said to occur primarily at higher elevations in the mountains of east, central, and northern Europe (McNeil 1976), and as far east as Nepal (Hara *et al.* 1982). Subsp. *leiocarpa* (Benth.) Hultén reportedly occurs from the Himalayas through China to Japan and the Bering Sea Islands (Hara *et al.* 1982); Takasu *et al.* (1980) recorded its occurrence in Japan, the Kuril Islands, Kamchatka, and Sakhalin. Subsp. *gigantea* (Nakai) Kitamura and subsp. *asiatica* Kitamura also occur in eastern Asia. In Japan, five varieties of *S. virgaurea* are recognized along with one closely related endemic species (Kitamura 1965).

Recent European floristic treatments (*e.g.*, McNeil 1976; Wagenitz 1979; Clapham *et al.* 1987) have recognized *Solidago virgaurea* as a single species with many varieties spread among several subspecies. Clapham *et al.* (1987, p. 841) noted that it is "Very polymorphic, with many named varieties differing in stature, pubescence, size, shape and serration of lvs, branching of infl. and size of individual heads." Detailed studies of east Asian plants also show the species to be markedly variable in vegetative and floral characters (Takasu *et al.* 1980). Transplant studies by Turesson (1925, 1930, 1931) showed that the species is highly plastic phenotypically as well as capable of forming locally adapted ecotypes. Experimental manipulation of ambient environmental factors demonstrated similar plasticity (Kawano & Takasu 1972).

Recent treatments of Chinese *Solidago* have recognized only three native species (Ling *et al.* 1985; Hu 1965-72). In contrast, however, to the conservative treatment of a single, highly variable *S. virgaurea*, a number of species are currently segregated from it in Russia, where 10-15 are said to exist (Kemularia-Nathadze 1938; Tamamschyan 1959; Cherpanov 1981). Further, as previously noted in the present paper, the morphological variability within east Asian *Solidago* extends across the boundaries of what are here considered several

subsections of sect. *Solidago*, and the recognition of a number of separate species may be justifiable. The taxonomy of Old World taxa of *Solidago* is badly in need of review and detailed study. With a clearer understanding there, the broader patterns of variation and the problems in inter-continental taxonomy can be addressed.

VARIATION IN *SOLIDAGO* - MORPHOLOGY OF THE CAPITULESCENCE

Cronquist (1980) observed that critical characters for identification of species of *Solidago* are in the nature of the capitulescence, the nature and disposition of the leaves, and the nature of the underground parts. Of these, however, the arrangement of the heads appears to be the most significant in the interpretation of phylogeny. Species of *Solidago* may be divided roughly into four groups, based on their general type of capitulescence: (1) corymboid, distinctly flat-topped, (2) thyrsoïd, a number of relatively elongated flowering branches forming a narrow to broad column, mostly above the well-developed cauline leaves, the lower branches sometimes distinctly elongated and independently thyrsoïd, (3) axillary, the flowering branches distinctly separated along the stem and shorter than subtending, well-developed, cauline leaves, and (4) the heads secund on the flowering branches, these ascending-recurved and forming a loose to relatively dense, pyramidal panicle.

Distinctly flat-topped capitulescences are characteristic of the generic groups hypothesized to be closely related to *Solidago* (Nesom 1991c), as well as of some species groups of the genus *Aster* L. that have features suggestive of a close relationship to *Solidago* (Nesom in prep.). Among the genera of the *Gutierrezia* lineage (Fig. 1), they are produced almost invariably. They are common among genera of the *Chrysothamnus* Nutt. and *Amphipappus* Torr. & Gray groups (Fig. 1), although the variability there in capitulescence form is considerably more pronounced than within the *Gutierrezia* lineage, ranging from dense, strictly flat-topped capitulescences of small heads to solitary and much larger heads. In some species of *Chrysothamnus*, as well as *Gutierrezia*, the capitulescence is opened into a broad panicle; a parallel modification has occurred in some groups of North American *Aster*, e.g., subg. *Symphotrichum* (Nees) A.G. Jones. The capitulescence of *Tonestus* and *Columbiadoria*, while often approaching corymboid, is commonly more open or tends to become racemoid. While this "relaxation" of the corymboid form produces capitulescences somewhat similar to those in *Solidago*, they do not appear to be homologous. This modification of form appears, instead, to be more analogous to that found in the *Heleastrum* group of North American *Aster*: most species produce a strictly corymboid capitulescence, but *A. hemisphericus* Alex. produces a racemose one, immediately derived from the corymboid form found in

its sister species, *A. paludosus* Ait. Corymboid capitulescences are produced in *Oligoneuron* and *Oreochrysum*, which have at times been included within the genus *Solidago*, as well as in a few species of *Solidago* sensu stricto (as recognized here): i.e., species in subsect. *Solidago*, subsect. *Thyrsoiflorae*, and subsect. *Junceae*; see comments above in the taxonomic section).

Because corymbs are the prevalent capitulescence type in every major group of American Solidagininae (except *Solidago*), as well as its potential ancestors, they appear to be the ancestral arrangement for the subtribe, and the few species of *Solidago* with such a capitulescence might be interpreted as relictual species retaining the primitive condition. The flat-topped capitulescences within *Solidago*, however, probably are not strictly homologous with those in the rest of the subtribe, this suggested by the observation that in the few *Solidago* species where they occur, they vary from flat-topped to rounded (capitate) or elongated (short-thyrsoid), thus approaching the more typical thyrsoid arrangement. Further, flat-topped capitulescences occur in three separate groups of *Solidago*, and if they are primitive within the genus, it would be necessary to postulate two independent transitions from a corymboid to thyrsoid capitulescence and one other from corymboid to paniculate-secund. This is possible, but it is simpler to assume that the thyrsoid form is primitive within *Solidago* (but derived within the subtribe from the corymboid form) and as such is an apomorphic feature allowing the recognition of *Solidago* as a monophyletic group. In this interpretation, flat-topped capitulescences in species of *Solidago* (sensu stricto) are secondarily and independently derived from thyrsoid ones characteristic of immediately related species.

Within *Solidago*, it is clear that "thyrsoid" and "axillary" capitulescences are closely related. Axillary clusters may be derived from a thyrsoid arrangement by a strong reduction in length of the flowering branchlets; the lower portion of a narrowly thyrsoid capitulescence sometimes breaks up into axillary clusters, and the distinction between the two types becomes somewhat arbitrary. The thyrsoid form is most similar to the corymboid one and most easily re-formed (apparently) into one that is flat-topped or nearly so.

The manner and evolutionary point of origin of the "secund" capitulescence within *Solidago* are not clear, but it is reasonable to assume that this specialized, asymmetrical form arose from a more symmetrical, thyrsoid ancestor. The secund form is found elsewhere in the Astereae particularly in the *Gutierrezia* lineage, where it has been independently derived in the monotypic genus *Thurovia* Rose and in some seemingly aberrant individuals of *Gutierrezia texana* (DC.) Torr. & Gray. The typical capitulescence in *G. texana* is paniculate, but the ancestral form for both *Gutierrezia* and *Thurovia* is corymboid. A similar capitulescence (secund) also occurs in some species of North American *Aster* (e.g., *A. ericoides* L., *A. lateriflorus* [L.] Britt.), where the immediately ancestral form also is more or less thyrsoid or broadly paniculate. Within *Solidago*, the secund capitulescence is here regarded as a specialization

delimiting a monophyletic group (identified as sect. *Unilaterales*).

In some species of *Solidago* sect. *Unilaterales* (e.g., subsect. *Maritimae*), the secund arrangement of heads may be obvious only in the lowermost branches of the capitulescence. In other species that typically produce a secund capitulescence (in various subsections, e.g., *S. mollis*, *S. lepida*, the *S. spectabilis* group), the heads instead sometimes appear to be borne in a broadened thyrs (but not at all flat-topped). Semple & Ringius (1983) observed that the capitulescence of *S. missouriensis* in Ontario is not secund although it is strongly so elsewhere in its range. The cause of such variability is not clear, but at least it is possible that it reflects an influx of genes from distantly related species within sect. *Solidago*. Hybridization occurs between species of sect. *Solidago* and sect. *Unilaterales* (Fernald 1950), and the hybrids produce capitulescences intermediate in morphology.

PHYLOGENETIC POSITION OF *SOLIDAGO*

A hypothesis regarding the phylogenetic position of *Solidago* and other genera closely related to it is shown in Figure 1. This generalized hypothesis is based on relatively few characters (Table 1) but ones that appear to be useful in indicating directions of phylogeny. The determination of polarities is based on observations above (regarding the capitulescence) and in the following discussion. Additional features of significance in delimiting the generic groups are discussed in the text. Some aspects of the present discussion were introduced earlier (Nesom 1991a, 1991b). The addition of the genus *Sericocarpus* (most recently placed in *Aster*) as a member of this group is discussed in Nesom (1993a). Earlier, I noted that the South American *Chiliotrichum* Cass. group was potentially among the close relatives of *Solidago* (Nesom 1991c), but this is clearly not the case (Nesom 1993b). The broader phylogenetic position of this and other extra-North American genera of Astereae will be considered in separate papers (Nesom in prep.).

The group of genera including *Solidago* in Fig. 1 appears to be holophyletic, and it is strictly equivalent to the Solidagininae, if that subtribe is accepted. This subtribe appears to be derived from ancestors closely related to *Aster* (Nesom in prep.). With two exceptions, the Solidagininae (in the present sense) is entirely North American: *Gutierrezia* has reached South America and radiated there, and *Solidago* has primitive species groups in both the New and Old Worlds as well as an endemic species in South America. This definition of the subtribe contrasts strongly with the corresponding group (in terms of genera and generic groups included) defined in the study by Zhang & Bremer (1993). Of the nine genera (each representing a generic group) included in their Solidagininae (their Figs. 2-4), only three are accepted in the present view: *Solidago*, *Petradoria*, and *Gutierrezia*. Of the other six, three

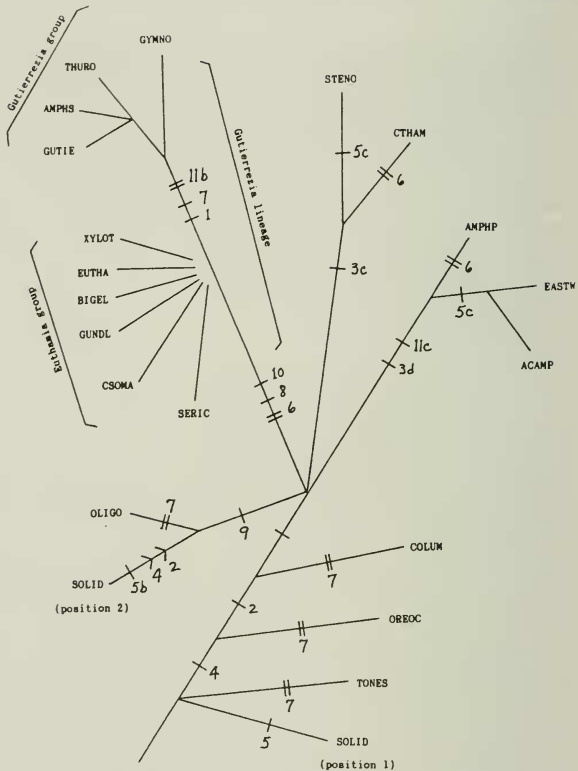


Figure 1. Phylogenetic hypothesis for subtribe Solidagininae (see further comments in text). The genera represented are the following: *Acamp-topappus* A. Gray (ACAMP), *Amphiachyris* (DC.) Nutt. (AMPHS), *Amphipappus* Torr. & Gray (AMPHP), *Bigelovia* DC. (BIGEL) *Chrysoma* Nutt. (CSOMA), *Chrysothamnus* Nutt. (CTHAM), *Columbiadoria* Nesom (COLUM), *Eastwoodia* Brandeg. (EASTW), *Euthamia* (Nutt.) Nutt. (EUTHA), *Gundlachia* A. Gray (GUNDL), *Gutierrezia* Lag. (GUTIE), *Gymnosperma* Less. (GYMNO), *Oligoneuron* Small (OLIGO), *Oreochrysum* Rydb. (OREOC), *Sericocarpus* Nees (SERIC), *Solidago* L. (SOLID), *Stenotus* Nutt. (STENO), *Thurovia* Rose (THURO), *Tonestus* A. Nels. (TONES), and *Xylothamia* Nesom *et al.* (XYLOT). Single slash = apomorphy; double slash = parallel apomorphy; back arrow = reversal.

Table 1. Characters and character states for subtribe Solidagininae (see further comments in text).

1. Base chromosome number, (a) $x=9$, (b) $x=5$ and 4
 2. Leaves, (a) stipitate-glandular or non-punctate, (b) resinous, punctate-glandular (except for *Chrysoma*, which is further derived; see Nesom 1991c and Anderson & Creech 1975)
 3. Leaf venation, (a) net-veined, (b) with 1-2 pairs of parallel veins, (c) with 3 strongly raised, parallel veins, (d) with a single, central nerve (midvein)
 4. Leaf margin, (a) toothed, (b) entire
 5. Capitulescence, (a) corymbose, (b) thyrsoid or secund, (c) solitary heads
 6. Heads, (a) mostly pedicellate, (b) mostly sessile, in glomerules
 7. Disc corolla lobes, (a) lanceolate, deeply cut, reflexing-coiling, (b) deltate, shallowly cut, erect
 8. Phyllaries, (a) without a strongly differentiated apical patch, the midvein usually more or less continuous from base to tip, (b) with a viscid apical patch, the midvein weak and visible only in the distal portion
 9. Phyllary veins, (a) without parallel resin ducts, (b) accompanied by orange resin ducts
 10. Achenes, (a) more or less elongated, strigose to glabrous, (b) turbinate, densely strigose-sericeous
 11. Pappus, (a) of bristles, (b) of awns or scales, these mostly strongly reduced, sometimes absent - the *Gutierrezia* group, (c) of awns or scales, these relatively elongated - the *Amphipappus* group
-

belong in the *Machaeranthera* Nees group (*sensu* Morgan & Simpson 1992): *Haplopappus* DC., *Corethrogyne* DC., and *Grindelia* Willd.; *Chrysopsis* (Nutt.) Ell. belongs in the goldenaster group (*sensu* Nesom 1991c); *Engleria* Hoffm. is closely related to the *Felicia* group; and *Pteronia* L. (considered by Zhang & Bremer to be closely related to *Engleria*) and *Ericameria* Nutt. are members of the subtribe Hinterhuberinae (*sensu* Nesom 1993b).

Apart from *Solidago* itself (with respect to capitulescence) and various other specialized taxa, the subtribe Solidagininae is characterized by a combination of the following features, most of which are correlated in their occurrence, and all of which have more specialized conditions within the group: (1) a base chromosome number of $x=9$, (2) leaves punctate, often resinous as well, mostly entire, (3) heads in a distinctly flat-topped (corymboid) capitulescence, (4) a pappus of capillary bristles (5) without a short, outer series, (6) ray flowers yellow, short, and few, or absent, (7) disc corollas abruptly broadened from the tube into the limb, the lobes narrowly lanceolate, deeply cut, and usually reflexing-coiling, (8) the collecting appendages of the disc style branches lanceolate, shorter than the stigmatic portion to nearly as long, with densely arranged sweeping hairs, the proximal hairs sometimes long-spreading but quickly reduced in length toward the style branch apex, where they commonly are no more than small papillae. Sometimes nearly all of the "sweeping hairs" are papilliform. All of these features occur in other Astereae, though not as a correlated group, and all except 2, 5, and 6 are apparently primitive among the Northern Hemisphere genera that are most closely related to the Solidagininae.

Within the Solidagininae, the "*Gutierrezia* lineage" is particularly coherent, comprising plants characterized by the following morphological features: (1) achenes small, turbinate, and densely strigose-sericeous, (2) heads sessile in glomerate clusters, and (3) phyllaries basally indurate, with a punctate or glutinous apical patch, the midvein weakly developed or inconspicuous. Additionally, all genera of the *Gutierrezia* lineage except *Sericocarpus* and *Chrysoma* have disc corollas abruptly expanded from a narrow tube into the limb and throat, the anther filaments inserted at the tube-limb junction. Similar corollas occur in various species of both major groups (sections) of *Solidago* as well as in species of *Chrysothamnus*. Outside of the Solidagininae, within North American Astereae, a similar corolla morphology also occurs in *Xanthocephalum* Willd. and its close relatives, where the corolla lobes are short relative to the limb — this variant has been referred to as "goblet shaped" (Lane 1982). With the lobes variably longer or shorter, abruptly ampliate disc corollas are also found in some species of *Erigeron* L., most genera of the Baccharidinae, most genera of Grangeinae as well as in Old World *Aster* and closely related genera. In fact, this corolla morphology is the most widespread among primitive elements of the Astereae.

The four genera of the "*Gutierrezia* group" form a group delimited by a reduced pappus, short disc corolla lobes, and a base chromosome number reduced from $x=9$ to $x=5$ and $x=4$ (*Gymnosperma* in this problematic interpretation is polyploid; currently under study). The specialized nature of these features is inferred from their correlated transition from states otherwise prevalent in the rest of the subtribe and from the coordinate phylogenetic status of the *Gutierrezia* group with the six genera of the "*Euthamia* group" (Fig. 1). Lane (1982) showed on the basis of morphology that the four genera of the *Gutierrezia* group are most closely related among themselves, and molecular evidence of Suh & Simpson (1991) provides corroboration of this relationship, showing additionally that these genera as a group are most closely related to the *Euthamia* group.

The genus *Solidago* (sensu stricto) can be identified by its thyrsoid (or secund) capitulescence, small, narrowly cylindrical to slightly fusiform achenes that are glabrous to sparsely strigose, and non-punctate leaves commonly with coarsely toothed margins. The leaf morphology and (to some extent) leaf disposition found in some species of *Solidago* are more similar to genera outside of the Solidagininae, such as *Heterotheca* Cass. and some groups of *Aster*, than to any other other genera of the *Gutierrezia* lineage (except for one species of the genus *Sericocarpus*, see Nesom 1993a).

The cladistic position of *Solidago* is somewhat equivocal, but the present study corroborates the previous suggestion that *Solidago* occupies a basal, and even perhaps isolated, position within the subtribe (Nesom 1991c). "Position 1" for it (Fig. 1) is the most parsimonious, given the assumptions that seem reasonable in the present study. In "position 2," two significant reversals must be assumed to have occurred in features otherwise characteristic of the subtribe: (1) the prominently toothed leaves prevalent among species of *Solidago* are secondarily derived from mostly entire ones, and (2) foliar punctations have been lost, then regained in a different form in two of the species. The molecular data of Suh & Morgan indicate that *Solidago* is more closely related to the strictly western North American elements of the subtribe than to the *Gutierrezia* lineage, but I have not been able to corroborate this on a morphological basis. This phylogenetic separation of *Solidago* is further emphasized by its geographic distribution: the primitive species groups are disjunct between Eurasia and eastern North America, and it is the only genus of Solidagininae that shows this pattern of ancient disjunction, one also found in *Aster* (Nesom in prep.).

As observed by Brouillet & Semple (1981), phyllary veins accompanied by conspicuous, parallel resin ducts occur in *Solidago*, *Oligoneuron*, and plants of the *Gutierrezia* lineage (mostly excluding the *Gutierrezia* group itself). The similarity in phyllary morphology is strongest between *Solidago* and *Oligoneuron*, and this is the only trait that might be regarded as a specialization shared by the latter two taxonomic groups. In fact, this feature must be empha-

sized if *Solidago* and *Oligoneuron* are placed as sister taxa. Dilated pappus apices occur in a few species of *Solidago* and one of *Oligoneuron*, but they also occur in *Acamptopappus*, *Amphiachyris*, all species of *Sericocarpus*, some of *Chrysothamnus*, and they are particularly common among primitive groups of *Aster* sensu lato hypothesized to be closely related to *Solidago*.

Amphipappus, *Eastwoodia*, and *Acamptopappus* are whitish-stemmed shrubs of the southwestern United States that produce uninervate leaves without any other conspicuous nervation and broad (scaly) pappus elements that are probably derived from lateral fusion of bristles (Lane 1988). The first two genera produce large, solitary heads and on this basis are placed here in close relationship, although Lane (1988) has observed that the evolutionary origin of each of these three genera may have occurred with more independence. This trio is closely related to the "*Chrysothamnus* group," which comprises *Chrysothamnus* Nutt., *Stenotus* Nutt., *Petradoria* E. Greene, *Hesperodoria* E. Greene, and *Vancleavea* E. Greene. The basic composition of this latter group was described by Lane (1988), although she also included *Ericameria*; Nesom (1991b) referred to a somewhat more restricted group of these genera as "the *Petradoria* group," but that name is no longer appropriate, since very recent studies of Nesom & Baird (1993) and Baird (in prep.) indicate that all of these genera except *Stenotus* should be incorporated in an expanded concept of *Chrysothamnus* and separated from *Ericameria*, which is part of a different phylad. The molecular data of Suh (1989) and Suh & Simpson (1990) indicate to some extent that the genera of the *Amphipappus* and *Chrysothamnus* groups are closely related among themselves, and their geographic and ecological proximity and tendency toward white-stemmed shrubbiness probably also reflect their closeness of ancestry. These plants possess features diagnostic of the Solidagininae, but there is considerable variability, particularly in capitular and floral morphology (see Nesom [1991a] and Baird [in prep.]), and even in style branch morphology, capitular size, and the number and length of rays, features generally more consistent within the rest of the subtribe.

Tonestus apparently occupies a relatively primitive position within the Solidagininae. It is the only genus beside *Solidago* with net-veined, prominently toothed leaves. The reduced capitulescences and white corollas produced in some species appear to be anomalous, although the latter perhaps are reflective of the ancestry of the subtribe. Although *Tonestus* and *Oreochrysum* differ significantly in many features, both produce phyllaries with foliaceous apices (see further comments below), but there is little else to indicate they might be closely related.

The anatomical data presented by Anderson (1972) and Anderson & Creech (1975) fit the phylogeny and classification of *Solidago* advanced here, including the segregation of *Oligoneuron* and *Oreochrysum*, without essential contradiction, although their sample of taxa was incomplete within the Solidagininae. They found that isolateral mesophyll is mostly restricted to *Solidago* sect. *Uni-*

laterales; it occurs as well in *Oligoneuron*. Secretory cavities are present in the leaves of many species of sect. *Unilaterales* but mostly absent in those of sect. *Solidago* (except subsect. *Solidago*). Secretory cavities also are absent in the leaves of both *Oligoneuron* and *Oreochrysum*.

STATUS OF *OLIGONEURON*

In an earlier study (Nesom 1991c), I regarded the species of *Oligoneuron* (segregated as a genus by Small [1903]) as a group within *Solidago*. A review of the features, however, of *Solidago* and its relatives in surrounding portions of the Astereae now appears to support treatment of *Oligoneuron* as a separate genus rather than a group within *Solidago* itself. *Oligoneuron* appears to be a primitive element within the subtribe (Fig. 1), without any specialization that would clearly ally it with the *Gutierrezia* lineage or with the *Chrysothamnus* or *Amphipappus* groups. Weber & Wittman (1992) noted that they regard *Oligoneuron* "as distinct a genus as *Petradoria*;" although they provided no supporting rationale, their comment almost certainly was intended to point out an analogous position for the two groups rather than one of close relationship.

A critical piece of evidence in the present interpretation of the phylogenetic (and taxonomic) position of *Oligoneuron* has been the observation that its leaves (except apparently for *O. rigidum* [L.] Small) are punctate, although the punctations are sometimes obscure, especially on the upper surface. This feature apparently has not been observed or mentioned in recent literature, even in the morphological and anatomical studies by Kapoor & Beaudry (1966) and Anderson & Creech (1975). The only reference to such that I have found is by Asa Gray (1884), who noted that the leaves of *O. nitidum* (Torr. & Gray) Small are punctate. Torrey & Gray (1842, p. 210) had earlier observed that plants of the same species "exude small quantities of resin when wounded," a phenomenon otherwise unknown in *Solidago* (although a few species are glandular or "glutinous"). Sunken punctations occur almost without exception in plants of the *Gutierrezia* lineage, where there is a minute glandular trichome ("Type C trichome," Nesom 1976) in the center of each one. The punctations of *Oligoneuron* are similar. In *Solidago*, foliar punctations occur only in the leaves of *S. odora* and *S. chapmanii*, where they appear to be derived independently from those of the *Gutierrezia* lineage, apparently lacking the central trichome and subtended by resin cavities different in anatomy (Anderson & Creech 1975). The only species of *Solidago* that produce conspicuous glandular trichomes similar to those of the punctatae are those of subsect. *Thyrsiflorae* (which see for further comments).

Phyllaries in *Oligoneuron* are broadly oblong to oblong-obovate, distinctively broader than any in *Solidago*, and each one usually bears 5-7 (or more) translucent, parallel veins running from the base to the very apex. In *O. album* and sometimes in *O. houghtonii*, only a single vein per phyllary may be

present. A few species of *Solidago* have veins lateral to the midvein, but they are weakly developed and visible usually only near mid-phyllary, not extending fully to the tip and base. Further, although the translucent veins of *Oligoneuron* are similar to those in *Solidago*, they tend to be distinctly paler in color than the strongly golden-yellow ones (colored by associated resin ducts) of the latter genus.

The achenes of all taxa of *Oligoneuron* are large, plump, glabrous, and the thin, whitish to brownish, longitudinal nerves are beneath the achene surface. These contrast with achenes of *Solidago*, which are smaller and more slender and elongated. The achenial nervation in sect. *Solidago* is more similar to that in *Oligoneuron*; achenial nerves in sect. *Unilaterales* are often distinctly raised and associated with orangish resin ducts that are barely or not beneath the fruit surface.

The taxa of *Oligoneuron* are clearly distinguished in morphology (corymboid capitulescence, punctate leaves, broad phyllaries "striate" with parallel veins, and plump and glabrous achenes) from those of *Solidago*. Only two instances of hybridization have been suspected between them, and both are equivocal in interpretation (see comments below regarding \times *Solidaster*). If the phylogenetic position of *Solidago* proves to be similar to "position 2" (Fig. 1), *Oligoneuron* might be retained as a primitive subgroup within *Solidago*, but there it would be removed phenetically as well as genetically (judging from the relative paucity of natural hybridization) from any possibly related species of the genus. Further, the inclusion of *Oligoneuron* within *Solidago* would suggest that two other disparate and apparently primitive species of Solidagininae (the monotypic *Oreochrysum* and *Columbiadoria*) might also be placed in *Solidago*, each in positions analogous to that of *Oligoneuron*. *Oligoneuron* is here regarded as a distinct genus, with taxonomy as follows.

Oligoneuron Small, *Fl. Southeast. U.S.* [ed. 1] 1188. 1903. [22 Jul]. *Solidago* subg. *Oligoneuron* (Small) House, New York State Mus. Bull. 254:693. 1924. LECTOTYPE, designated here: *Solidago rigida* L.

Solidago sect. *Corymbosae* Torr. & Gray, *Fl. N. Amer.* 2:208. 1842.
LECTOTYPE, designated here: *Solidago rigida* L.

A. *Oligoneuron* sect. *Oligoneuron*

Various authors have referred to "sect. *Oligoneuron*" within *Solidago* (e.g., Gleason & Cronquist 1963; Correll & Johnston 1970; Brouillet & Semple 1981), but there is no indication that any such nomenclatural combination has ever been made formally. Semple (1992b) recently noted that the correct name at that rank within *Solidago* is sect. *Corymbosae* Torr. & Gray.

Rhizomes short; leaves net-veined, minutely punctate (distinctly to obscurely, or not so in most forms of *Oligoneuron rigidum*), entire to serrulate, the basal and lower spatulate with a long petiole, the cauline epetiolate, lanceolate or oblanceolate, barely reduced upward; heads in a distinctly flat-topped (corymboid) capitulescence; phyllaries with 3-5 (or more) parallel veins; rays yellow; achenes glabrous, 5-7 (10-20) nerved; pappus bristle apices attenuate.

Species included (Beaudry 1963; Semple & Ringius 1983; Heard & Semple 1988):

1. *Oligoneuron rigidum* (L.) Small, *Fl. Southeast. U.S.* 1188. 1903. BASIONYM: *Solidago rigida* L., *Sp. Pl.* (ed. 1) 880. 1753. (see Heard & Semple [1988] for complete synonymy).
 - a. *Oligoneuron rigidum* (L.) Small var. *rigidum*.
 - b. *Oligoneuron rigidum* (L.) Small var. *humilis* (T.C. Porter) Nesom, *comb. nov.* BASIONYM: *Solidago rigida* L. var. *humilis* T.C. Porter, U.S. Dept. Interior Misc. Publ. 4:63. 1874.
 - c. *Oligoneuron rigidum* (L.) Small var. *glabrata* (E.L. Braun) Nesom, *comb. nov.* BASIONYM: *Solidago rigida* L. var. *glabrata* E.L. Braun, *Rhodora* 44:3. 1942.
2. *Oligoneuron ohioense* (Riddell) G.N. Jones, *Trans. Illinois Acad. Sci.* 35:63. 1942. BASIONYM: *Solidago ohioensis* Riddell, *Syn. Fl. West. States* 57. 1835.

B. *Oligoneuron* sect. *Ptarmicoidei* (House) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Ptarmicoidei* House, *New York State Mus. Bull.* 254. 710. 1924. TYPE: *Aster ptarmicoides* Nees.

Unamia E. Greene, *Leafl. Bot. Observ.* 1:6. 1903. [24 Nov]. TYPE: *Oligoneuron album* (Nutt.) Nesom.

Rhizomes short; leaves parallel-veined, minutely punctate (distinctly to very obscurely in *Oligoneuron houghtonii* and *O. album*), entire to serrulate, the basal and lower oblanceolate without a well-defined petiole, the cauline oblanceolate, gradually reduced upward; heads in a distinctly flat-topped (corymboid) capitulescence; phyllaries with 3-5 parallel veins; rays yellow or white; achenes glabrous, 5-7 nerved; pappus bristle apices attenuate or clavate.

- * *Oligoneuron* ser. *Ptarmicoidei* (House) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Ptarmicoidei* House, New York State Mus. Bull. 254. 710. 1924. TYPE: *Aster ptarmicoides* Nees.

Ray flowers with white ligules, the pappus bristle apices distinctly clavate, and the phyllaries with a single, distinctly raised, central vein, commonly expanded near the apex into a broad gland-like structure.

3. *Oligoneuron album* (Nutt.) Nesom, *comb. nov.* BASIONYM: *Inula* (*Chrysopsis*) *alba* Nutt., *Gen. N. Amer. Pl.* 2:152. 1818. *Diplopappus albus* (Nutt.) Lindl. ex Hook., *Fl. Bor.-Amer.* 2:21. 1834. *Heleastrum album* (Nutt.) DC., *Prodr.* 5:264. 1836. *Aster albus* (Nutt.) A. Eat. & J. Wright, *N. Amer. Bot.* 147. 1840. Not Willd. ex Spreng. 1826. *Eucephalus albus* (Nutt.) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:299. 1841. *Unamia alba* (Nutt.) Rydb., *Fl. Rocky Mts. & Adj. Plains* 878. 1917. *Doellingeria ptarmicoides* Nees, *Gen. Sp. Aster.* 183. 1832. The epithet of this species in the genus *Doellingeria* Nees was proposed by Nees as a substitute for Nuttall's original, which should have been adopted. *Doellingeria* "*ptarmicoides*" Nees is thus superfluous and illegitimate, and subsequent combinations based on it must also be considered illegitimate. *Aster ptarmicoides* (Nees) Torr. & Gray, *Fl. N. Amer.* 2:160. 1841. *Unamia ptarmicoides* (Nees) E.L. Greene, *Leafl. Bot. Observ.* 1:6. 1903. *Solidago ptarmicoides* (Nees) Boivin, *Phytologia* 23:21. 1972. Not *S. alba* Miller 1768.

- * *Oligoneuron* ser. *Xanthactis* Nesom, *ser. nov.* TYPE: *Oligoneuron riddellii* (Frank) Rydb.

Differt a *O.* ser. *Ptarmicoidei* (House) Nesom praecipue ligulis luteis.

Ray flowers with yellow ligules, the pappus bristle apices slightly clavate (*Oligoneuron houghtonii*) to attenuate, and the phyllaries with several parallel veins (often 1-veined in *O. houghtonii*).

Species included:

4. *Oligoneuron nitidum* (Torr. & Gray) Small, *Fl. Southeast. U.S.* 1188. 1903. BASIONYM: *Solidago nitida* Torr. & Gray, *Fl. N. Amer.* 2:210. 1842.
5. *Oligoneuron riddellii* (Frank) Rydb., *Fl. Prairies & Plains Central N. Amer.* 799. 1932. BASIONYM: *Solidago riddellii* Frank in Riddell, *Syn. Fl. West. States* 57. 1835.

Solidago amplexicaulis Martens, Bull. Acad. Roy. Sci. Bruxelles 8:68. 1841. Not Torr. & Gray ex Gray 1884.

6. *Oligoneuron houghtonii* (Torr. & Gray ex Gray) Nesom, *comb. nov.* BASIONYM: *Solidago houghtonii* Torr. & Gray ex Gray, *Man. Bot. N. U.S.* (ed. 1) 211. 1848.

Oligoneuron album is *Aster*-like in general appearance (leafy stems, long, white rays on relatively large heads), and the species has been treated in *Aster* and as a monotypic genus (see taxonomic summary above). Boivin (1972) transferred it to *Solidago*, noting the high incidence of hybridization between it and other species of *Solidago* (= *Oligoneuron*). In its phyllary morphology, also, it is more similar to *Solidago* but not to any species of *Aster sensu lato* (Brouillet & Semple 1981); each phyllary has a translucent midvein nearly continuous from base to apex and sometimes an additional pair of similar, lateral veins. Anderson & Creech (1975) found a close similarity in leaf anatomy between *O. album* and the species of the *Oligoneuron* group, and Brouillet & Semple (1981) have summarized morphological, chemical, and geographical data in support of the treatment of this species within the *Oligoneuron* group. Jones (1980) excluded the species from *Aster* in her classification of the New World species.

Putative hybrids between *Oligoneuron album* (or any other species of *Oligoneuron*) and species of *Solidago* have been reported only between *O. album* and *S. canadensis*, and the interpretation of these is strongly equivocal (see below). In contrast, *O. album* is known to form natural hybrids with three yellow-rayed species of sect. *Oligoneuron* (Bernard 1969). Morton (1979) hypothesized that the hexaploid genome of *O. houghtonii* may even include that of *O. album*, the former species originating in an ancestral hybridization event between *O. album* and *O. ohioense*. As noted by Brouillet & Semple (1981), however, *O. album* and *O. houghtonii* are more similar to *O. riddellii*, a species not considered by Morton, in their 3-veined and strongly basally disposed leaves, and the latter is more likely to have been involved with *O. album* in the parentage of *O. houghtonii*.

Interspecific hybrids within *Oligoneuron* have been named as *Solidago*. They are formally transferred to *Oligoneuron* with the following combinations:

1. *Oligoneuron* × *lutescens* (Lindl. ex DC.) Nesom, *comb. nov.* BASIONYM: *Diplopappus lutescens* Lindl. ex DC., *Prodr.* 5:278. 1836. *Diplopappus albus* [var.] *lutescens* [Lindl. ex DC.] Hook. ex Torr. & Gray, *Fl. N. Amer.* 2:160. 1841. The indication of varietal status, as implied by Hooker (*Fl. Bor.-Amer.* 2:21. 1834) was not validly published. *Solidago* × *lutescens* (Lindl. ex DC.) Boivin, *Phytologia* 23:22. 1972. *Aster*

- lutescens* (Lindl. ex DC.) Torr. & Gray, *Fl. N. Amer.* 2:160. 1841. *Unamia lutescens* (Lindl. ex DC.) Rydb., *Bull. Torrey Bot. Club* 37:147. 1910. (*O. alba* × *O. rigida*).
2. *Oligoneuron* × *krotkovii* (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *krotkovii* Boivin, *Naturaliste Canad.* 94:647. 1967. (*O. alba* × *O. ohioense*).
 3. *Oligoneuron* × *bernardii* (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *bernardii* Boivin, *Phytologia* 23:21. 1972. (*O. alba* × *O. riddellii*).
 4. *Oligoneuron* × *maheuxii* (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *maheuxii* Boivin, *Phytologia* 23:21. 1972. (*O. riddellii* × *O. rigida*).

STATUS OF THE INTERGENERIC HYBRID × *SOLIDASTER*

× *Solidaster* Wehrhahn in Bonstedt, *Pareys Blumeng.* (ed. 1) 2:525. 1932. [described as a hybrid between *Aster* and *Solidago*].

× *Asterago* Everett, *Garden. Chron.*, ser. 3, 101:6, fig. 2. 1937. [*nom. illeg.*].

Solidaster × *luteus* M.L. Green ex Dress, *Baileya* 20:33. 1976. Brouillet & Semple (1981) treated the hybrid as a species of *Solidago* but made the nomenclatural transfer using an invalid name (*Solidaster luteus* "M.L. Green" vs. *Solidaster luteus* "M.L. Green ex Dress"). Articles by Yeo [1971] and Dress [1976, 1979] present the rationale for the belated validation of the name by Dress.

The original hybrid, which was thought to have been produced from an accidental cross between a naturalized *Solidago* and cultivated *Aster*, was discovered around 1910 in a nursery in Lyon, France (Ruys 1931; Bernard 1969). It was fertile and seeds of its progeny were sent to George Arends in Germany, who further propagated it. Arends (1931, p. 190) described the results: "The seedlings showed great diversities in colour and habit of growth. Some plants were nearly true *Aster ptarmicoides*, others being long and slender like a *Solidago*, and showing all shades of color from nearly pure white to golden yellow." It is clear, particularly from these early, first-hand descriptions, as well

as from the morphology of the plants, that "*Aster*" *ptarmicoides* (= *Solidago ptarmicoides* = *Oligoneuron album*) was one of the parents of \times *Solidaster*.

In his investigation of the parentage of \times *Solidaster*, Bernard (1969) reasonably considered other taxa of *Solidago* (sensu lato) besides *Oligoneuron album* that were known to occur as natives or adventives in the area of Lyon, based on a published regional flora cited by him: four native taxa of the *Solidago virgaurea* L. complex (*Solidago* subsect. *Solidago*) and a group of North American species naturalized in the area, including *Solidago caesia* L. and *Solidago flexicaulis* L. (each identified by a synonym, both in *Solidago* subsect. *Glomeruliflorae*), *Solidago canadensis* L., *Solidago gigantea* Ait., and *Solidago arguta* Muhl. (all of sect. *Unilaterales*), *Solidago rigida* (= *Oligoneuron rigidum*), and *Solidago graminifolia* (L.) Salisb. (= *Euthamia graminifolia* [L.] Nutt.). These taxa also are included in broader floristic treatments of the region (e.g., McNeil 1976; Wagenitz 1979), although they have not included *Solidago caesia* or *Solidago flexicaulis*. From among these candidates, Bernard chose *Solidago canadensis* as most likely for the second parent of \times *Solidaster*, but he provided few details regarding the selection process. Bernard did not specify what segment of the variable *S. canadensis* he was referring to, nor is it possible to decide from his characterization of that species. Further, his table of morphological comparisons between the two putative parents and the hybrid dealt with features that are not exclusive to either of his choices of parents. Although he noted that his hypothesis regarding the parentage was "fragile," it has not heretofore been reconsidered. Brouillet & Semple (1981) accepted the hybrid as a cross between *Solidago canadensis* and *Solidago ptarmicoides* (see further comments below).

Although Yeo (1971) did not question hypotheses regarding the parentage of \times *Solidaster*, he published observations on its morphology (pp. 29-32) contrasting with Bernard's approach: it "differs from *Solidago* in its almost perfectly symmetrical inflorescence, long pedicels, absence of clustering of capitula, and the pale ray corollas; from *Aster* it differs in its usually very small capitula and its yellow ray florets." The "capitula [are] not at all clustered, the branches not recurved or secund." Certainly, there is no hint of the distinctive capitulescence of secund branches characteristic of most forms of *Solidago canadensis* (also of *Solidago gigantea* and *Solidago arguta*) to be found in the hybrid, and although the capitulescence of \times *Solidaster* was described as "pyramidal" (Bernard 1969), no one has contradicted Yeo's accurate observation regarding its symmetry and lack of secund branches.

Solidago lepida DC. (perhaps = *Solidago elongata* Nutt.), which is sometimes treated within *Solidago canadensis*, produces small heads that are barely, if at all, secund on the branches of the capitulescence. In habit and disposition of leaves, it is a reasonable candidate for the parentage of \times *Solidaster*, but its leaves are not glutinous, the phyllaries are lanceolate with a single sunken vein and are not at all thickened even toward the base, and the disc corollas are

gradually broadened in width upward. Finally, *Solidago lepida* is not known to occur in Europe and must also be eliminated on this basis.

Of remaining European candidates for the second parent of \times *Solidaster*, *Solidago virgaurea* is improbable because of its relatively thin, non-viscid, basally disposed, distinctively petiolate leaves with serrate margins, virgate (though sometimes broad) capitulescence, relatively large heads, acute phyllary apices, and long ligules. The naturalized *Solidago caesia* and *Solidago flexicaulis* are also unlikely because of their highly distinctive capitulescence as well as other features.

Of all the species considered here as the second parent of \times *Solidaster*, *Euthamia graminifolia* best fits the expected morphology, particularly in its combination of (1) rhizomatous habit, (2) distinctly glutinous, narrow, mostly entire, and predominantly cauline leaves, (3) basally indurate phyllaries, (4) heads borne near the branch tips, not at all secund, and (5) goblet-shaped disc corollas. There are problems in this interpretation of parentage, most significantly the lack of obvious foliar punctations in the hybrid (present in both putative parents), the more conspicuously reticulate foliar venation (inconspicuous in both parents), and the more dense vestiture of longer hairs than usually found on either parent. A comparison of significant features of the hybrid and its putative parents is presented here.

The origin of the hybrid remains problematic and the unequivocal identification of its parents probably will require its experimental reconstruction. This is especially critical if it is not morphologically intermediate but more like one of the parents than the other. Indeed, many features of *Oligoneuron album* appear to be heavily weighted in the hybrid. In view of the hypotheses considered here regarding the generic status of *Oligoneuron* and the parentage of \times *Solidaster*, the plants known as \times *Solidaster* are still regarded as a true intergeneric hybrid, but one in which neither of the probable parents (*Oligoneuron* and *Euthamia*) is represented in its nothogeneric name ("condensed formula").

STATUS OF A PUTATIVE HYBRID INVOLVING *OLIGONEURON* *ALBUM* FROM CANADA

A plant recently collected from eastern Canada (Bruce Co., Ontario: *Semple & Brammall 2775 - WAT!*), has been identified by Semple as a hybrid between *Solidago canadensis* and *Oligoneuron album* (= *S. ptarmicoides*). The label indicates that this plant was the only one of its kind seen in the area but that *O. album*, *S. hispida*, and *S. juncea* were common there. The plant is clearly a *Solidago*, and it might be regarded as a small individual of *S. canadensis* aberrant in vestiture, leaf morphology, capitulescence, and other features. Its only features that could be construed as a contribution from *O. album*, the

HYBRID:

Habit: many stemmed from the base, probably rhizomatous.

Leaves: basal absent, the cauline even in size, not reduced upward, weakly 3-nerved with conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, not punctate but strongly glutinous.

Phyllaries: thick and basally indurate, midvein \pm continuous but thickened above, greatly narrowed below.

Receptacle: alveolate.

Heads: numerous, small, short pedicellate, borne near the branch tips in a broad panicle, often approaching corymboid.

Disc corollas: abruptly ampliate above the narrow tube, lobes long.

Style branches (disc flowers): lanceolate and flattened, apices merely papillate.

Achenes: sparsely strigose with very short hairs.

Pappus bristle apices (disc flowers): slightly dilated.

OLIGONEURON ALBUM:

Habit: 1-few stemmed from the base.

Leaves: basal persistent, the cauline strongly reduced upward, strongly to weakly 3-nerved, without conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, inconspicuously punctate, sometimes glutinous.

Phyllaries: thick and basally indurate, midvein \pm continuous but thickened above, greatly narrowed below.

Receptacle: alveolate.

Heads: few, large, long-pedicellate, solitary but in broad corymbs.

Disc corollas: gradually widened upward, lobes short.

Style branches (disc flowers): linear and somewhat terete, hispid from base to tip.

Achenes: glabrous.

Pappus bristle apices (disc flowers): dilated.

EUTHAMIA GRAMINIFOLIA:

Habit: many stemmed from the base, rhizomatous.

Leaves: basal absent, the cauline even in size, not reduced upward, strongly 3-nerved, without conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, conspicuously punctate, often strongly glutinous.

Phyllaries: thick and basally indurate, midvein only visible distally, not at all raised.

Receptacle: fimbriate.

Heads: numerous, small, sessile, borne in glomerules at the branch tips, in broad corymbs.

Disc corollas: abruptly ampliate above the narrow tube, lobes long.

Style branches (disc flowers): lanceolate and flattened, apices merely papillate.

Achenes: strigose.

Pappus bristle apices (disc flowers): attenuate.

whitish ligules and dilated pappus apices, are also found in *S. bicolor* and *S. hispida*, both of which occur in Ontario, although *Semple & Brammall 2775* shows little morphological affinity to either of those. It is hardly similar to *S. juncea*, nor can it be identified as any species reported from Ontario (Semple & Ringius 1983) or anywhere else. It might be a hybrid in which the synergy of a peculiar combination of genes has masked its parentage, but since one of the parents (*vide* Semple's interpretation) was not in the area of its putative hybrid offspring, there is no compelling reason that the other should have been there. Although neither *S. canadensis* nor *O. album* can be unequivocally eliminated as a parent, there is little evidence to indicate that either, and especially the latter, was involved.

The following description briefly characterizes *Semple & Brammall 2775*: stems 3 from the base, slender and ascending, 28-37 cm tall, unbranched below the capitulescence, glabrate; leaves glabrate, weakly 3-veined but strongly reticulate, narrowly oblanceolate, shallowly serrate, not punctate or resinous, all cauline (the few near the base withered), evenly distributed and becoming shorter upward; capitulescence a small (ca. 17-22 heads), dense, nearly capitate, terminal cluster 2.0-2.5 cm wide and 2-3 cm long; heads 4-5 mm wide, the longest phyllaries 3.0-3.5 mm long, on filiform pedicels 2-4 mm long; phyllary midvein not expanded distally; disc flower style branches with triangular-deltate collecting appendages; ray flowers with creamy ligules ca. 2 mm long; achenes immature but apparently glabrous; pappus bristles slightly clavate at the apex.

STATUS OF THE MONOTYPIC GENUS *OREOCHRYSUM*

Oreochrysum Rydb., Bull. Torrey Bot. Club 33:152. 1906. TYPE and only species: *Solidago parryi* (A. Gray) E. Greene = *Haplopappus parryi* A. Gray = *Oreochrysum parryi* (A. Gray) Rydb.

In recent floristic treatments, this species is variously treated within *Haplopappus* or *Solidago* or as a monotypic genus. In a recent study (Nesom 1991c), I maintained it within *Solidago*, but further observations have convinced me that its treatment as a monotypic genus is the most appropriate. The segregation of *Oligoneuron*, the only other group besides *Oreochrysum* with corymboid capitulescences that has recently been included within *Solidago*, and the conclusion that the thyrsoid capitulescence probably is primitive within *Solidago*, have been significant in formulating the decision regarding *Oreochrysum*. Hybrids between *Oreochrysum* and any other species of *Solidago* or *Oligoneuron* have not been reported.

In his transfer of *Haplopappus parryi* to *Solidago*, Greene (1894) observed that it is "near" *S. multiradiata* (subject. *Solidago* in the present treatment),

but he also noted similarities between it and *S. macrophylla* as well as the taxa of *Oligoneuron*. Rydberg (1906) noted that *Oreochrysum* resembles *Oligoneuron* in habit, but (p. 152) "the character of the involucre and the style appendages, however, distinguish it from *Oligoneuron* as well as from *Solidago* proper." Hall (1938) rejected its placement in either *Solidago* or *Oreochrysum* and maintained it as a monotypic section within *Haplopappus*. In its combination of corymboid capitulescence, disc flowers with narrowly funnellform corollas and short, erect corolla lobes, long style appendages of the disc flowers, and particularly in its barely graduated phyllaries without a continuous midvein (the outer often completely foliaceous), it is significantly removed in morphology from any putatively close relatives in *Solidago*, although reasonably close matches can be found for some of its individual features. On a morphological basis, *Oreochrysum* is set apart from *Solidago* primarily on the basis of its phyllary morphology and arrangement, and its markedly corymboid capitulescence, in combination with a suite of other characters unusual for *Solidago*.

Oreochrysum and *Tonestus* were distinguished as a pair in keys by Rydberg (e.g., 1917) based on their common production of phyllaries with foliaceous apices. The molecular data of Morgan & Simpson (1992) further suggest that *O. parryi* is more closely related to *Tonestus* than to *Solidago* itself. Plants of *Oreochrysum* and *Tonestus*, with a few in subsect. *Thyrsiflorae* (sect. *Solidago*), are the only ones among North American Solidagininae that produce glands on stipes above the leaf surface.

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